

# Hypervariable or hyperdiverse, an independent assessment of the taxonomically confusing land snail genus *Tropidophora* (Pomatiidae: Littorinoidea: Caenogastropoda) in Madagascar\*

John Slapcinsky

Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.

Correspondence, John Slapcinsky: [slapcin@flmnh.ufl.edu](mailto:slapcin@flmnh.ufl.edu)

**Abstract:** The terrestrial littorinoid snail genus *Tropidophora* Troschel, 1847 is especially diverse on Madagascar with 94 currently recognized species and numerous named varieties. Supposed high within-species variation in shell and genital morphology led some researchers to suggest that these characters may be too variable to distinguish species, prompting them to conclude that the group may be taxonomically over-split. Recent sampling allows an independent test using COI sequence data which suggests that Madagascar's *Tropidophora* species are not over-named but are more diverse than previously thought. Molecular diversity is congruent with traditional morphology-based species concepts suggesting that future work using both molecular and morphological data sets will be useful in a taxonomic revision of the genus.

**Key words:** littorinoid, DNA barcoding, shell variation

Land snails are one of the most successful groups of terrestrial animals, second only to arthropods, with an estimated 35,000 to 64,000 species, only about 24,000 of which are described (Lydeard *et al.* 2004). Gastropods of at least eight major lineages have invaded land, some more than once (Rosenberg 1996). With no life stage capable of active long distance dispersal, land snails are notable for having high levels of geographic variation and genetically structured populations. This is especially true of larger species for which passive dispersal by wind, rafting, or transport on other animals is especially difficult. Land snail species are readily isolated and regional diversity can be quite high. Early surveys reporting high snail diversity in temperate habitats combined with anecdotal evidence of low diversity in tropical habitats led to the hypothesis that relatively cool, moist temperate areas with their associated deep leaf litter would have higher snail diversity than the tropics (Solem 1984), a pattern unlike most other plant and animal groups. However, recent surveys suggest that low abundance and incomplete sampling is responsible for this perceived pattern and that land snails in the tropics are often quite diverse (Schilthuizen 2011). The considerable field effort required to sample low abundance taxa has not only challenged macro-ecological studies but has also slowed species discovery and the taxonomic description of these species.

Perhaps the best documented tropical land-snail fauna is that of Madagascar, which was monographed by Fischer-Piette *et al.* (1993, 1994), who compiled all previously known taxa and described many additional species using the relatively meager collections available at that time. Between 1990 and 2009 Ken Emberton embarked on large-scale field studies, sampling approximately 1500 stations across the island. By 2003, 28 families, 77 genera and 685 species were reported from Madagascar (Pearce 2003). Later generic revisions (Emberton 2002a, 2002b, 2003a, 2003b, 2003c, 2003d, 2004, 2007) and field surveys (Emberton 2009, Emberton and Griffiths 2009a, 2009b, Emberton *et al.* 2010, Griffiths and Herbert 2013) brought the species total to approximately 1100, nearly equal to the 1200 species found in North America, north of Mexico, but in less than 3% of the land area. Even so, there are several groups collected in these surveys that have not been monographed, including one of the island's most diverse and taxonomically difficult groups, the pomatiid land snail genus *Tropidophora* Troschel, 1847.

*Tropidophora* are terrestrial littorinoid snails endemic to the east African coast and Indian Ocean islands of the Comoros, Mascarenes, and Seychelles where there are relatively few species, and Madagascar where the genus is particularly diverse. Madagascar's *Tropidophora* are found in eastern rainforests, northern and western deciduous forests and

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limestone *tsingys* (eroded limestone outcrops), and southern spiny thickets, but not in the open grassy and savannah habitats which often isolate these forests and outcrops. This patchwork of isolated habitats probably plays a role in the rich diversity of this and other groups in Madagascar (Quéméré *et al.* 2012).

The last treatment of Madagascar's *Tropidophora* (Fischer-Piette *et al.* 1993) recognized 94 species while treating 24 previously recognized species and 17 new forms as varieties of *Tropidophora tricarinata* (Müller, 1774) and seven species and one new form as varieties of *Tropidophora semidecussata* (Pfeiffer, 1847). These two species are highly variable in size, shape, color, and banding pattern and are distributed nearly island-wide, unlike other species of *Tropidophora*. Remarking on the need for independent data to evaluate the high level of shell variation within these and other *Tropidophora* species, Emberton (1995) developed a phylogenetic hypothesis for nine species from 40 populations using allozyme data. Comparing shell and genital characters from the same populations with the resulting cladogram, he concluded that high levels of within-species variation exist in both morphological data sets, thus these characters were too variable to unravel species level relationships and suggested that many more species and forms should be synonymized. However, the cladogram was poorly resolved and relied on few presumed synapomorphies to define species. Many of the populations treated as conspecifics in Emberton's analysis were considered different species by authors prior to Fischer-Piette's monograph. Therefore, if current species concepts are in fact complexes of multiple species, then high levels of "intra-specific" variation would be expected in the morphological data sets. It is still unclear if *Tropidophora* species are currently over-split because of high intraspecific variation as suggested by Emberton (1995) or if intraspecific variation appears remarkably high because of lumping of previously recognized species. Testing these alternative hypotheses requires independent data.

Emberton's field surveys collected 4400 specimen lots of *Tropidophora* from 1100 of his 1500 sampling sites, some live collected and alcohol preserved. This material was deposited at Florida Museum of Natural History at the University of Florida (UF) and specimens were selected to build a COI sequence library for terrestrial snails as part of a DNA Barcoding project to develop a species-level identification tool for land snails (Hebert *et al.* 2003). To date, 188 sequences have been generated for 60 nominal *Tropidophora* species. Here I use these data to test whether *Tropidophora* contains high levels of intraspecific shell variation or many unrecognized species. Rapidly describing the diversity of these forests is particularly important because Madagascar's high rate of deforestation has resulted in the loss of 40% of the islands forest cover since the 1950's (Harper *et al.* 2007), threatening species restricted to forested habitats with extinction.

## MATERIALS AND METHODS

All 4400 specimen lots of *Tropidophora* collected in Emberton's surveys along with approximately 100 lots from other sources were sorted and specimens mature enough and in sufficiently good condition to identify were grouped into approximately 200 recognizable morphospecies based on shell characters. Each morphospecies was matched with a species or variety name using Fischer-Piette *et al.* (1993) or given a numerical designation if they could not be clearly matched. Sixty morphospecies were identified among the 188 specimens that were subsequently successfully sequenced. Of these, 29 could be assigned to *Tropidophora* species and eight to varieties of *Tropidophora tricarinata* recognized by Fischer-Piette (1993). The remaining 23 morphospecies included 16 clearly undescribed taxa and seven others which could not be unambiguously assigned to species or named variety without further taxonomic study and generic revision. Of the 23 numerically identified morphospecies, ten fit within the broad concept of *T. tricarinata* and would be considered varieties of that species based on Fischer-Piette's concept.

Approximately 2 mm<sup>3</sup> pieces of foot tissue were cut from alcohol-preserved specimens, extracted with DNazol (Molecular Research Center, Inc., Cincinnati), and a 658 bp fragment of the cytochrome c oxidase subunit I (COI) was amplified by polymerase chain reaction (PCR) using primer pairs LCO-1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO-2198 (5'-TAAACTTCAGGGTGACCAAAAATCA-3') as described by Meyer (2003), and sequenced at the Interdisciplinary Center for Biotechnology Research (ICBR) at the University of Florida. Other tissue samples were extracted, amplified by PCR and sequenced at the Canadian Centre for DNA Barcoding (CCDB), using their standard procedures. Voucher data, including images, georeferenced localities, and sequences are available from the Biodiversity of Terrestrial Snails (TSB) project stored at the Barcode of Life Data System (BOLD, [www.barcodinglife.org](http://www.barcodinglife.org)) (Ratnasingham and Hebert 2007). Sequences were aligned by eye in Bioedit (Hall 1999). Nucleotide substitution models were calculated using hierarchical Likelihood Ratio Tests using ModelTest 3.7 (Posada and Crandall 1998) as implemented in PAUP (Swofford 2003). Two Bayesian analyses were conducted in MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) using the general time reversible model with invariant sites and gamma distribution of rates across sites (GTR+I+G) based on ModelTest results. The two independent runs of 2 and 3 million generations were distributed over five chains, four heated and one cold. The temperature parameter was raised to 0.05. Trees were sampled every 1000 generations. Burn-in was 200 trees and run convergence was assessed by comparing the mean and variance of log likelihoods, both by eye and by examination of split frequencies. A maximum likelihood analysis using the



same model of evolution was performed using Randomized Accelerated Maximum Likelihood (Stamatakis *et al.* 2008). Intraspecific and interspecific genetic distances were calculated using a Kimura 2-Parameter model (K2P).

## RESULTS AND DISCUSSION

All 60 morphospecies identified using shell characters were clearly separated in the COI trees from both Bayesian analyses (only one shown here, Fig. 1) and from the Maximum Likelihood analysis. The three analyses did not differ in the composition of terminal taxa but differed slightly in the position of several taxa and clades with low posterior probabilities ( $< 0.70$ ) or bootstrap values ( $< 0.50$ ). The 46 morphospecies represented by more than one sample were all reciprocally monophyletic, demonstrating that shell characters are not too variable within species to provide useful information in species delineation. In fact, morphological characters appear also to be useful in predicting species relationships, as shown by the clustering of morphologically similar taxa within well supported clades. For example, species in the clade composed of *Tropidophora* sp. 14, *T. sp.* 205, *T. virgata* (Sowerby, 1843) and *T. consocia* (Pfeiffer, 1848) all have high-spined straw-yellow shells with multiple dark bands and share similar habitats and geographic distributions in dry deciduous forests in far northern Madagascar. Similarly, the species in the clade composed of *T. aspera* (Potiez and Michaud, 1838), *T. thesauri* Fischer-Piette, 1949 and *T. moulinsii* (Grateloup, 1840) all have large, dark colored and banded, low-spined and strongly striated shells and inhabit northern deciduous forests. Even species within morphologically variable clades share unique characteristics. The clade that contains the largest species of *Tropidophora*, the strongly carinate *T. cuvieriana* (Petit de la Saussaye, 1841), also contains the relatively small lirata species *T. lirata* (Pfeiffer, 1852) and *T. denselirata* Fischer-Piette, Blanc and Salvat, 1969. All members of this clade (sp. 112–*T. virgo*) share a uniquely reflected and internally thickened peristome, a likely synapomorphy for the group, and are distributed in deciduous forests in northern Madagascar.

Even within the broadly defined *T. tricarinata* complex, several clades can be separated using shell morphology. Taxa in *T. tricarinata* clade 1 (Fig. 2) inhabit northern rainforests and possess weakly striate but not carinate shells that are banded and have an orange-red stain on the columella that appears to be a synapomorphy for the group. The low-spined, smooth and striped taxa in *T. tricarinata* clade 5 are also morphologically similar and inhabit far south-eastern rainforests. Clades 2, 3, and 4 contain taxa that are restricted to north-eastern, central-eastern and south-eastern rainforests respectively,

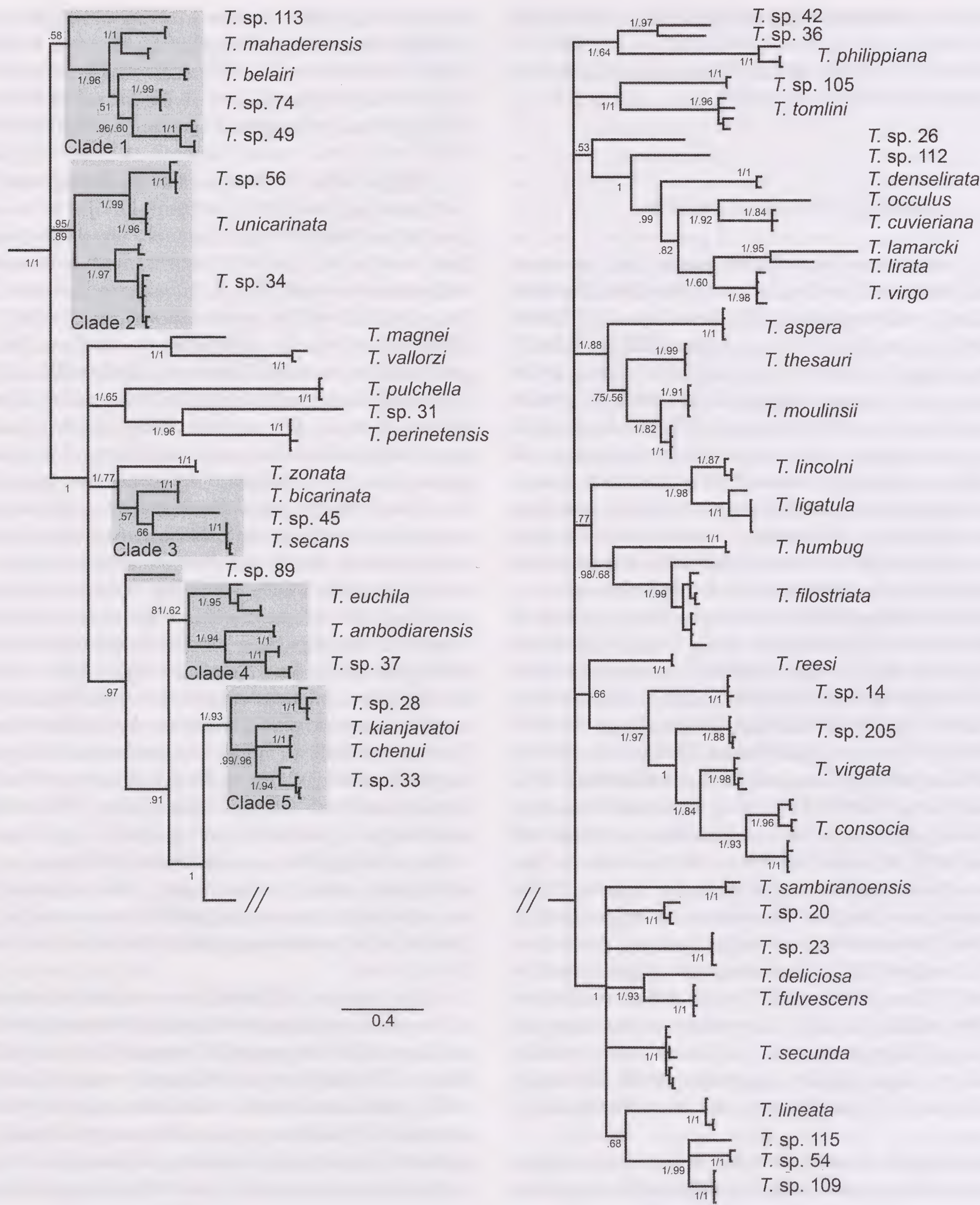
but unlike the other *T. tricarinata* clades these taxa are morphologically quite variable. One of the most variable shell characters are the raised ridges for which the genus *Tropidophora* (keel bearer) is named and for which the species *T. tricarinata*, and its supposed varieties *T. bicarinata* (Sowerby, 1843) and *T. unicarinata* (Lamarck, 1822) are also named.

If most large *Tropidophora* from Madagascar's eastern rainforests are one highly polymorphic species as suggested by Fischer-Piette (1993), then molecular data should show that 'varieties' of *Tropidophora tricarinata* are monophyletic with respect to other *Tropidophora* species. Likewise, sympatric individuals of this species should be genetically similar because they have the opportunity to interbreed and are not reproductively isolated. However, if shell variation is not random and if taxa synonymized into, or named as varieties of *T. tricarinata* are in fact reproductively isolated species, then morphologically similar taxa should cluster into reciprocally monophyletic genetic groups that may occur sympatrically.

While traditionally-defined species were recovered as monophyletic groups in both the Bayesian and Maximum Likelihood analyses, the taxa synonymized into *Tropidophora tricarinata* form a paraphyletic assemblage at the base of the tree, so that a clade that includes all of them also includes all of the other sequenced *Tropidophora* species. Varieties in this complex were distributed among five major clades (Fig. 1, clades 1–5). Clade 3 also includes *T. zonata* (Petit de la Saussaye, 1850), a species not considered a variety of *T. tricarinata* by Fischer-Piette (1993). Two clades of other *Tropidophora* species, one composed of *T. magnei* Fischer-Piette, Blanc, Blanc and Salvat, 1993 and *T. vallozzi* Fischer-Piette, Blanc, Blanc and Salvat, 1993 and the other consisting of *T. pulchella* (Sowerby, 1843), *T. sp.* 31 and *T. perinetensis* Fischer-Piette and Bedoucha, 1965 form a polytomy with clade 3, nesting between clades 1, 2 and 4. Even if these species were to be synonymized with *T. tricarinata* the resulting 'species' would remain paraphyletic with respect to all remaining *Tropidophora*.

The 'varieties' of *Tropidophora tricarinata* are recognizable as morphospecies, are reciprocally monophyletic in COI, and have different geographic ranges. The taxa within each clade of *Tropidophora tricarinata* vary more in height/width ratio, presence and number of carinae, and color pattern than any other *Tropidophora* species. For example, clade 2 includes taxa with high-spined bicarinate and low-spined unicarinate shells. Clade 3 encompasses taxa with high-spined shells that are smooth or bicarinate and a low-spined taxon with a tricarinate shell. Likewise, clade 4 also includes low and high-spined forms. The other clades, while less variable in shell shape and sculpture, vary markedly in color. In most groups of snails, including other *Tropidophora* species, this level of morphological variation usually indicates multiple species and in fact many of these *Tropidophora tricarinata* varieties were originally described as species.



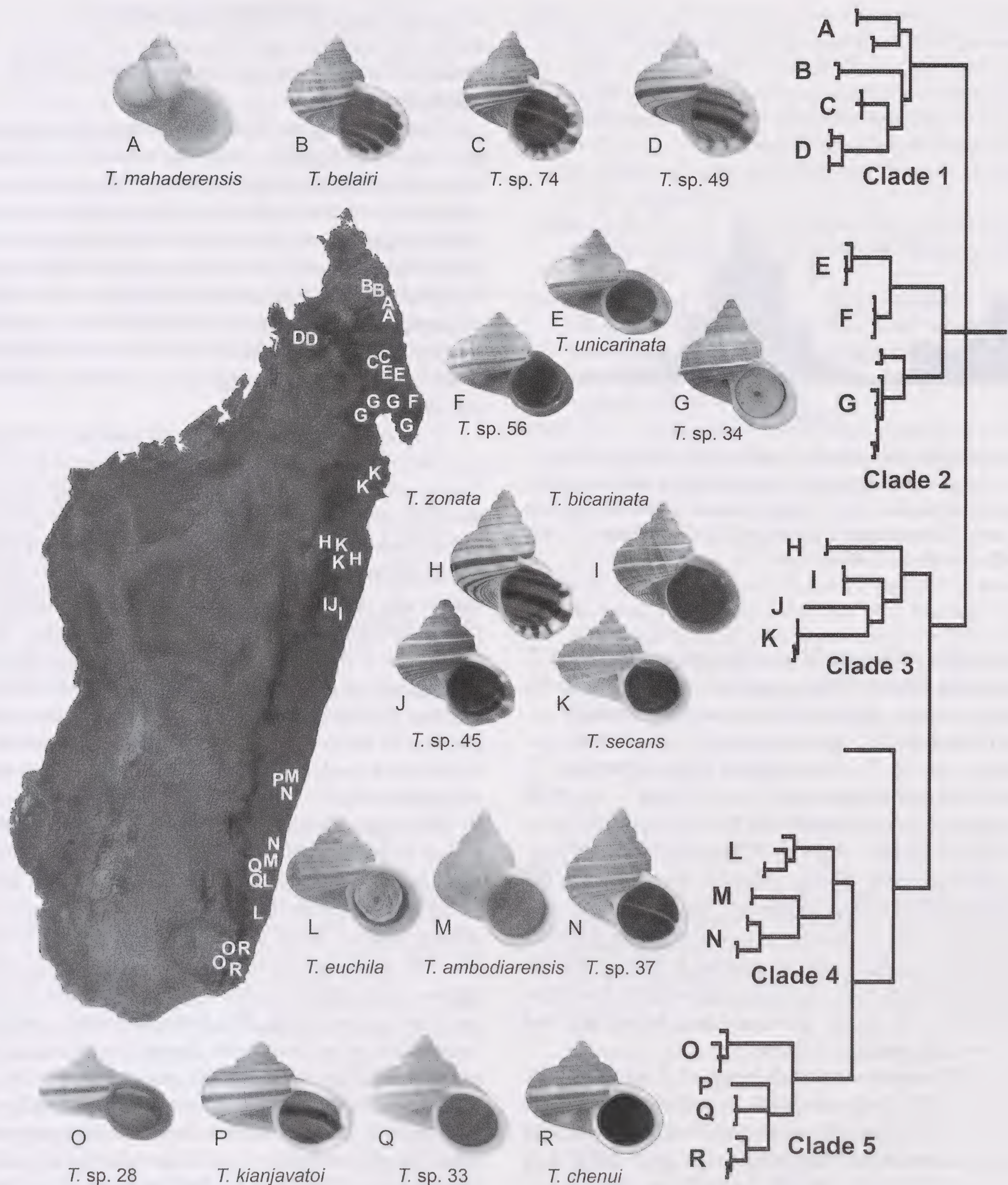


**Figure 1.** Majority rule Bayesian inference tree for Madagascan *Tropidophora* based on COI sequence data. Posterior probabilities (left) and Maximum Likelihood bootstrap values are given for nodes with greater than 50% support (right). Clades composed of *Tropidophora tricarinata* varieties are highlighted in gray. Branch lengths are measured in expected substitutions per site. Tree rooted with *Pomatias elegans* (Müller, 1774), not shown.

Intraspecific variation in COI sequence data is also particularly high within *Tropidophora tricarinata* as defined by Fischer-Piette (1993) especially when compared to older species

concepts. Intraspecific variation in COI sequence data within traditionally defined species averages 1.97% ( $SE = 0.05\%$ ) while interspecific variation averages 12.06% ( $SE = 0.02\%$ ).





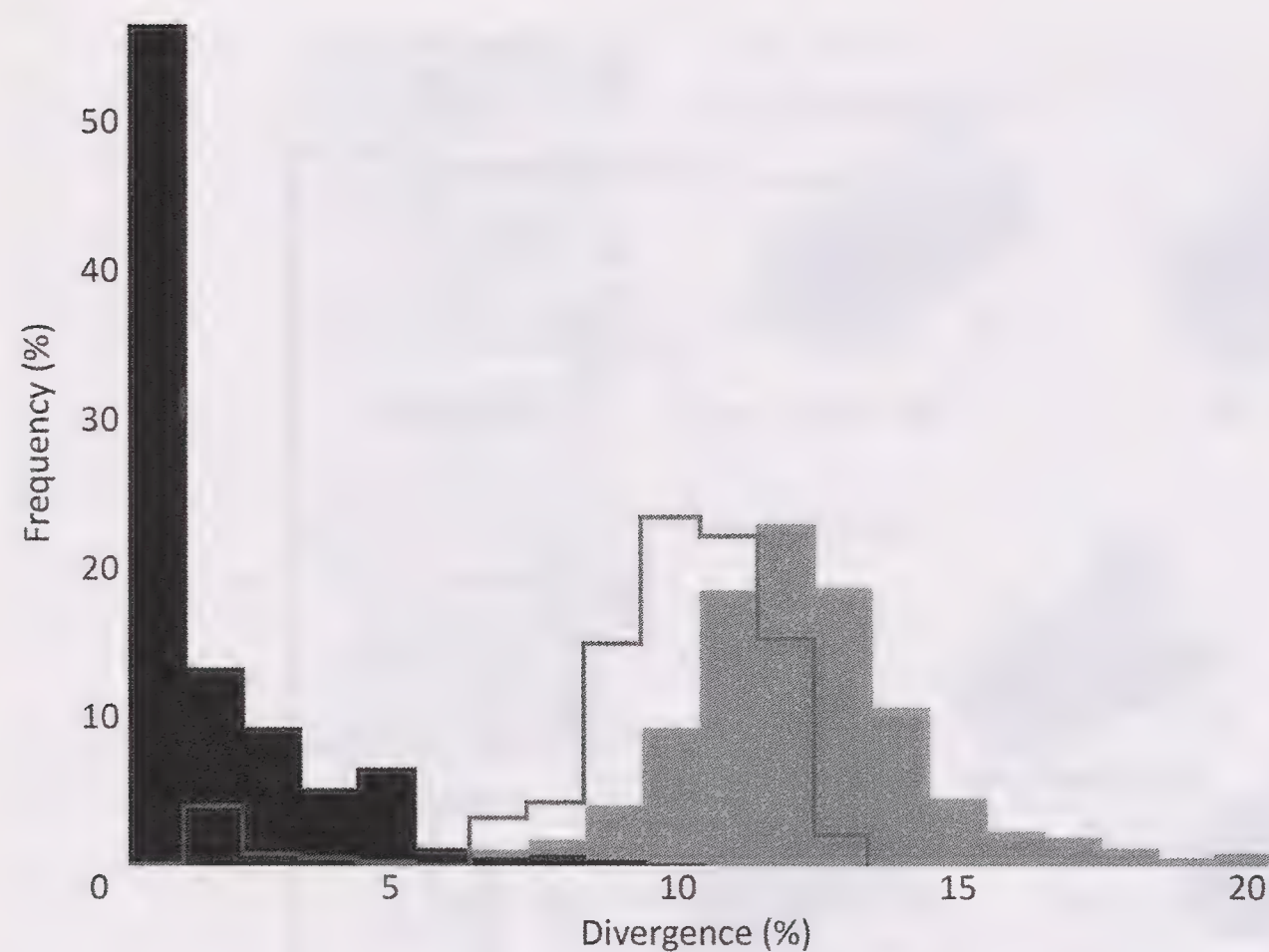
**Figure 2.** Clades of *Tropidophora* taxa attributed to *Tropidophora tricarinata* with their geographic distributions. (Color shown in electronic version only).

There is relatively little overlap in intraspecific and interspecific variation between 7–10% (Fig. 3). Conversely, intraspecific variation within the taxa synonymized by Fischer-Piette into *Tropidophora tricarinata* averages 10.04% ( $SE = 0.06\%$ ) and is bimodal, one peak falling within the intraspecific variation of

the traditionally defined species and another peak largely overlapping interspecific variation in the genus.

Recent and extensive sampling by Emberton allows explicit tests of reproductive isolation between taxa considered varieties of *Tropidophora tricarinata* by Fischer-Piette (1993).





**Figure 3.** Distribution of normalized intraspecific (black) and interspecific divergences (solid gray) for *Tropidophora* based on species concepts prior to Fischer-Piette (1993) compared with intraspecific variation within *Tropidophora tricarinata* (gray outline) as envisioned by Fischer-Piette (1993).

Several pairs of taxa that would be attributed to varieties of *T. tricarinata* using Fischer-Piette's species concept occur in the same 20 x 20 meter study plots and were successfully sequenced. These include *T. bicarinata* and *T. sp. 45* from Andriantanteley Massif, *T. secans* Fischer-Piette, 1949 and *T. zonata* in Zahamena Reserve; and *T. sp. 37* and *T. sp. 89* at Vatovavy Reserve. Each of these pairs have the opportunity to interbreed yet maintain unique shell characters and COI haplotypes, demonstrating genetic isolation, thus meeting the strictest definition of biological species. This is the most convincing evidence that *T. tricarinata* is a complex of different species and not one highly variable species. It is likely that the other named varieties of *T. tricarinata* that are not known to be sympatric but are equally divergent morphologically and genetically are also species level taxa.

Uncritically relying on a small group of characters to define species is likely to be deceptive in a diverse group like *Tropidophora*. Better sampling combined with independent sequence data demonstrate that some of the most visible shell characters used to group *Tropidophora tricarinata* varieties are taxonomically misleading, including the disposition of carinae for which the group was named. Superficially similar bicarinate shells *T. sp. 34*, *T. bicarinata*, *T. sp. 45* and *T. sp. 37* are found in three of the five clades of *T. tricarinata*, two of these are found microsympatrically. Bicarinate shells are also found in other *Tropidophora* species including *T. occlusa* (Mörch, 1852) and *T. cuvieriana* and this character is either symplesiomorphic or has evolved multiple times, and is, therefore, of limited phylogenetic utility. While the congruence

of morphologically defined taxa with COI sequence data shows that morphological characters are useful for defining species, it is also clear that some of these characters can be misleading.

Synonymizing multiple morphologically disparate species into *Tropidophora tricarinata* resulted in a 'taxon' that was morphologically highly variable. This confusing variation combined with limited fluid-preserved material for anatomical investigation or DNA analysis, resulted in the perception that the group was too challenging to revise (Verdcourt 1993). Congruence of COI data with morphologically-based species concepts suggests that COI sequence data is providing reliable information and that a revision of the group using a combination of morphological and genetic information is possible.

If nearly all species and named varieties of *Tropidophora tricarinata* are in fact species, then there are 143 described *Tropidophora* species in Madagascar, although those named as varieties after 1961 are not available names and will need to be re-established. Furthermore, there are approximately 60 additional morphospecies in collections that do not match any currently recognized species or named variety, which appear to be undescribed species-level taxa. This would bring the total number of species for the genus in Madagascar to approximately 200, more than doubling the number of currently recognized species. Modern taxonomic revision of the group combining shell and anatomical characters with molecular data will be needed to test these suppositions.

Madagascar's historically fragmented forest habitats have played an important role in the development of the islands diverse fauna (Quéméré *et al.* 2012). The land snail fauna is no exception; with more than 1100 species it is probably the most diverse mollusk fauna of any similarly sized terrestrial area. However, deforestation threatens these and other forest-adapted species with extinction. Most of Madagascar's conservation areas are chosen using data from surrogate species, usually vertebrates, rather than more diverse invertebrate groups like snails, despite the fact that snails and insects are better predictors of conservation priorities for vertebrates than the converse (Moritz *et al.* 2001). Unfortunately, poor taxonomy and until recently, sparse sampling have limited the use of snails in these conservation efforts. The availability of increasingly inexpensive sequence data is proving invaluable in rapidly uncovering species complexes, which can be efficiently targeted for taxonomic revision and detailed study. Unraveling the taxonomy of complex groups will uncover diversity that can be used to prioritize natural area conservation efforts as well as making these species accessible for evolutionary, ecological and other scientific investigation. These efforts are badly needed especially in species-rich and poorly-sampled tropical habitats that are rapidly undergoing profound habitat alteration.



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